

If the time of every spike is important, the number of distinct response patterns is substantially larger than the number of spikes, theoretically making it possible for response patterns to encode much more information than that in spike count alone. In the simplest model, there would be $n^k/k!(n-k)!$, that is, n choose k , different ways of placing k spikes in n time bins. The large number of the potentially available degrees of freedom has led both experimentalists and theoreticians to consider whether spike patterns measured with millisecond precision carry information that has not yet been identified. Detecting whether and which patterns carry information is difficult, however, if n choose k really indicates the number of degrees of freedom in a neuronal response. Although exact jittering provides an extraordinary number of distinct patterns (more than 1,000,000 for 3 spikes in 200 ms), only if particular patterns are consistently present in responses elicited by particular stimuli do they transmit information.

In a provocative speculation, a proposal has been made that particular types of spike patterns across neurons might play a critical role in higher brain functions, such as the perception of objects (Abeles, 1991; Lestienne, Strehler, 1987; Lestienne, Tuckwell, 1998; von der Malsburg, Schindler, 1986). To investigate implications of this speculation, Oram et al (1999) recently carried out the information theoretical and statistical studies of the precisely timed spike patterns described below. The investigators used three types of previously studied exactly timed spike patterns (Lestienne, Strehler, 1987; Abeles et al., 1993; Abeles, Gerstein, 1988):

1. triplets for which the exact same pattern repeated one or more times (called repeating triplets below);
2. repeating quadruplets (defined in the same manner as the repeating triplets, except the patterns used four spike times), and
3. the numbers of each type of triplets occurring during all presentations of a particular stimulus.

Here we discuss the results from the repeating triplets, which are representative of those from all three types of exactly-timed spike patterns

examined.

First, the information carried in the spike count alone was compared with the information carried by the spike count plus the numbers of repeating triplets. Despite the triplets carrying some stimulus-related information, the joint code carried only the same amount of information as that carried by the spike count alone.

The information-theoretical analysis shows that the number of triplets is strongly related to the spike count. Therefore, a model was sought to connect the spike count to the exactly-timed spike patterns. Several such models have been proposed. These models share the assumption that the exact times of spikes are randomly determined, but differ in the distribution from which spike times are drawn. The most common class of models uses a Poisson process (originally uniform, time-varying more recently) to determine the spike times. The time-varying Poisson process maintains the appropriate peri-stimulus-time histogram (PSTH), but fails to match the distribution of spike counts and interspike intervals. Other models match the distribution of spike counts. Randomly reordering the interspike intervals within a train maintains the interval distribution but not the PSTH; exchanging spikes between trains maintains the PSTH, but not the interval distribution; and jittering the times of spikes in trains retains both parameters approximately but neither exactly. Thus, each model preserves some important features of the response, but none preserves all (Table 1).

The numbers of precisely timed patterns found in the spike trains that were generated using these models have failed to match the numbers in experimentally observed spike trains. This result has led researchers to reject their models and to tentatively conclude that at least some precisely timed spike patterns are determined by the stimulus condition (Abeles et al., 1991; Aertsen et al., 1991; Zhang et al., 1997; Lestienne, Strehler, 1987; Lestienne, Tuckwell, 1998; Prut et al., 1998). It is possible, however, to retain the assumption of stochasticity and to conclude instead that the models of spike time distributions are not adequate.